

BULB MORPHOLOGY IN SOME WESTERN NORTH AMERICAN SPECIES OF ALLIUM

DALE W. McNEAL, JR.

Department of Biological Sciences, University of the Pacific,
Stockton, California 95204

MARION OWNBEY

Department of Botany, Washington State University, Pullman 99163

The circumboreal genus *Allium* includes about 80 species in North America. Within this group nine well defined alliances are recognized (Ownbey and Aase, 1955; Saghir et al., 1966). This paper presents the results of a study of bulb morphology and seasonal development in the *Allium acuminatum* alliance and in selected species of the *A. falcifolium* and *A. kunthii* alliances. Numerous external bulb characters are used in the classification of *Allium* but little is known about their detailed morphology or development. In the only recent systematic study of bulb morphology, Mann (1960) demonstrated the naturalness of the European section *Molium* using comparative bulb morphology of six species in the section. Data presented here demonstrate that a very close relationship exists among species in the *A. acuminatum* alliance. They also support the observation, based on chromosome numbers, floral morphology, and other characters, that most of the New World species of *Allium* are closely related (Ownbey and Aase, 1955).

Members of the *Allium acuminatum* alliance have a generally uniform morphology, although major groups and subgroups are recognizable (McNeal, 1970). The alliance is marked by the strong sclerification of the inner epidermal cells of the inner leaf base. The cell walls become thickened, eventually forming a moisture retaining bulb coat with a characteristic pattern of cellular reticulation on its surface. Differences in the organization and development of the bulb allow recognition of two major species groups, one of which develops rhizomes while the other is non-rhizomatous.

In the rhizomatous group each bulb produces one to three rhizomes. A new bulb is borne terminally on each rhizome with the subsequent disappearance of the parent bulb. Within this group two subgroups are recognized: in the first, the rhizomes are short, not exceeding 2 cm in length, including the new bulbs. This subgroup includes *Allium bolanderi* Wats., *A. dictuon* St. John, and *A. mirabile* Hend. The second subgroup includes only *A. unifolium* Kell. with rhizomes up to 5 cm long. In the non-rhizomatous species of the alliance (*A. acuminatum* Hook., *A. amplexans* Torr., *A. crispum* Greene, *A. davisiae* Jones, *A. dichlamydeum* Greene, *A. hickmanii* Eastw., *A. hyalinum* Curran, *A. lacunosum* Wats., *A. peninsulare* Lemmon, *A. praecox* Bdg., and *A. serratum* Wats.), all

new growth occurs within the preceding year's bulb coats. All of these species have similar bulb morphology and no subgroups are recognized here.

The bulb morphology of *Allium acuminatum* was described by Mullen (1928). The present investigation confirms Mullen's work, extends it to include all of the non-rhizomatous species in the alliance, and compares the morphology of the rhizomatous and non-rhizomatous species. Because of their similar rhizomatous habit, two other species, *A. crenulatum* Wieg. of the *A. falcifolium* alliance, with short rhizomes, and *A. glandulosum* Link and Otto, of the *A. kunthii* alliance, with long rhizomes, were also examined.

MATERIALS AND METHODS

Representatives of all species of the *Allium acuminatum* alliance were collected in the western United States (Table 1) and cultivated either in the greenhouse or experimental garden at Pullman, Washington, or in the garden at Stockton, California. Their seasonal development was observed over a period of several years. Two methods were used to ascertain bulb structure and development; dissection of whole, live or preserved plants under a low power microscope and preparation of stained microsections from bulbs embedded in paraffin.

Material of *A. unifolium*, *A. bolanderi*, and *A. mirabile* was collected at 10 day intervals from 1 Jan. 1968 to 8 Apr. 1968 and again on 20 July 1968. Three other species, *A. dictyon*, *A. crenulatum*, and *A. glandulosum*, were collected after anthesis when the new bulbs were mature. The bulbs were killed in F.A.A. (formalin-acetic acid-alcohol), dehydrated through a tertiary butyl alcohol series, and embedded in paraffin using standard techniques (Johansen, 1940). Following embedding, serial sections, 10 microns thick were cut from each bulb. The sections were mounted on slides and stained in 0.1% solution of safranin in 50% alcohol for 18–24 hours and 0.2% solution of fast green in 95% alcohol for 5–10 seconds (Brooks, Bradley, and Anderson, 1963). Bulbs of all species were collected at various times and dissected while fresh or after preservation in F.A.A., or observed in the serial microsections to verify the structure and development sequences reported by Mullen.

RESULTS

A survey of all of the non-rhizomatous species of the *Allium acuminatum* alliance indicated no essential differences in their organizations or seasonal development. The following description is based on Mullen's 1928 study and on observations made during the present investigation.

Figure 1 is a diagram of a median-longitudinal section through a bulb of *Allium acuminatum*. It represents a bulb collected just after the resumption of growth in the early spring. The outer bulb coat, R, is a brown, yellow-brown, or gray, heavily sclerified resistant or protective

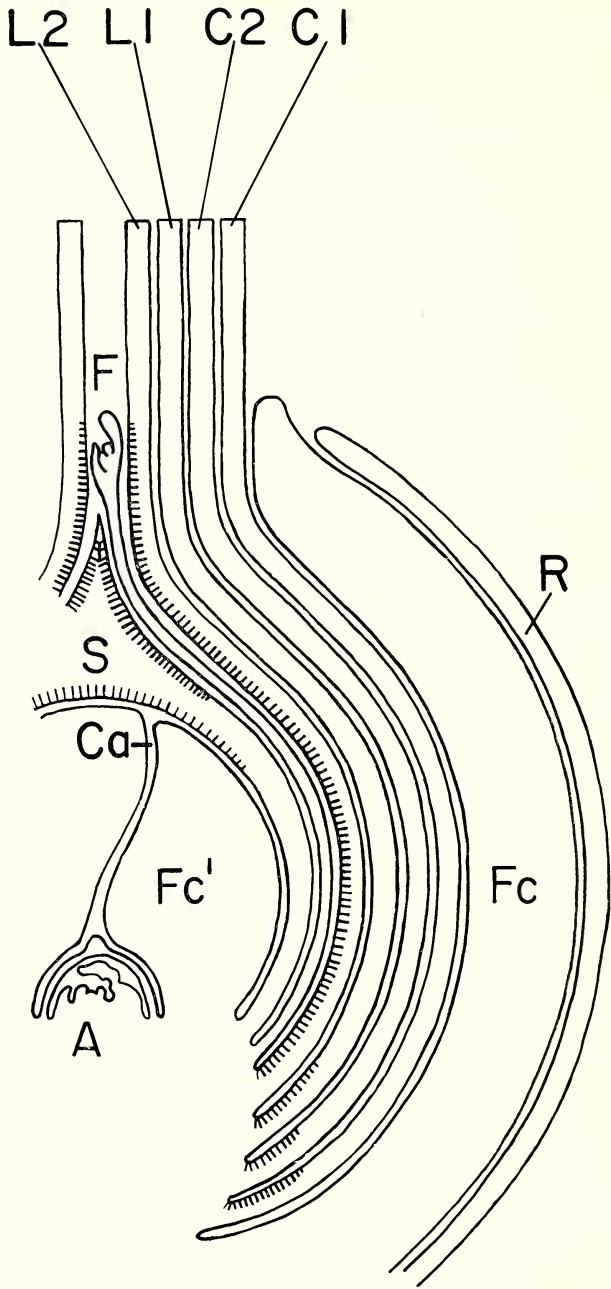


FIG. 1. Median-longitudinal section through the bulb of *Allium acuminatum* (After Mullen, 1928): A, apical meristem; Ca, canal; S, sheath; F, scape (current year); Fc', new fleshy cataphyll; Fc, old fleshy cataphyll; L1, L2, leaf bases; C1, C2, cataphyll bases; R, resistant layer.

layer. It was formed through the modification of the inner epidermis of the previous year's inner leaf base. This layer corresponds to the shaded portion of L2 in the diagram. It is all that remains of the foliar organs produced by the primary axis during the preceding growing season, the other leaf tissues having disintegrated in the intervening period. The resistant layer is one cell thick with the sclerified cell walls forming a characteristic reticulate pattern on the surface. The pattern depends on the size, shape, and arrangement of the epidermal cells forming the layer. (In *A. acuminatum*, for example, the cells are isodiametric, being either square or polygonal. In *A. crispum* they are elongate and rectangular in shape and arranged in vertical rows, so oriented as to give the appearance of a herringbone pattern; in *A. hyalinum*, on the other hand, the cells are elongate, but irregularly arranged and not forming any regular pattern.)

Not shown in Figure 1, but frequently observed in bulbs at this stage, is the dried basal portion of the previous year's scape. If present, it is located immediately inside the resistant layer, in a position corresponding to F in the present year's growth.

In *Allium*, as in almost all monocotyledonous plants, the inflorescence terminates the primary axis (Holttum, 1955). The *Allium* bulb is a highly condensed shoot on which the foliar organs arise from the apical meristem in an acropetal sequence. The scape develops immediately above the upper foliage leaf with a secondary axis forming below the scape in the axil of this leaf. Figure 1, then, represents this secondary axis that has developed into a new bulb, thus serving to continue the plant that produced it. Since the plant axis is composed of at least two branches, it is a sympodium. Strictly vegetative plants having only a primary axis are monopodial.

The first leaf of the secondary axis is a closed, bladeless, sheathing bulb scale located inside the resistant layer and corresponding to S in Figure 1. Since this sheath is disrupted when growth is resumed in the spring, it is usually present only as fragments and frequently is not recognizable at all. The sheathing bulb coat (S, fig. 1), is the first leaf of the tertiary axis that will develop into next year's bulb.

The fleshy cataphylls (Fc and Fc') are the second leaves of the secondary and tertiary shoot axes respectively. They are typical tunicate bulb scales. The fleshy cataphyll of the present season (Fc') will constitute the bulk of next year's bulb and is a storage organ, chiefly of water. The fleshy cataphyll of last year (Fc) is distended, accommodating the new vegetative growth that is developing inside. This cataphyll remains firm until early March when it begins to disintegrate, the remaining nutrients presumably being translocated to the new growth.

The open end of the developing fleshy cataphyll (Fc') forms a tubular canal (Ca) that leads from the apex to the base of the cataphyll and is enlarged below around the shoot apex (A). As new leaves develop from

the shoot apex they extend up this canal until, in the following spring, Fc' becomes distended, resembling the fleshy cataphyll of the preceding year (Fc) as shown.

Two non-fleshy cataphylls (C1 and C2) are located inside the fleshy cataphyll. Below ground they resemble the bases of the foliage leaves (L1 and L2); above ground they are colorless sheathing membranes. If the above-ground portion of the plant had been included in Figure 1, C1 and C2 would be shown as closed, nested tubes, enclosing the tips of L1 and L2. As the growing season progresses the foliage leaves elongate rapidly, breaking through the tips of the cataphylls, and appear as concave-convex leaf blades with sheathing bases. The two cataphylls persist as sheathing membranes at the base of the foliage leaves.

The sheathing base of the inner leaf (L2) forms a cylindrical passageway, extending to a point above ground where the leaf sheath ends and the blade begins. The inflorescence (F) which terminates the shoot axis, grows up through this passageway from its point of origin along the union between the sheath (S) and the inner leaf base.

The sheath, as noted earlier, is the first leaf of an axillary branch that will develop into next year's bulb. It is a fairly thin cataphyll, snugly enclosing the fleshy cataphyll; its apical portion is thickened and conical and extends into the cylindrical passageway formed by L2.

The cataphylls (C1 and C2) and the outer leaf base (L1) show slight development of resistant thickening at their bases, but it is the inner epidermis of L2 that develops this thickening to the greatest extent, forming, eventually, the resistant layer, R. The sheath (S) shows the same modification on both the inner and outer surfaces.

During the winter months the epidermal cells that will form the resistant layer appear identical with other epidermal cells of the plant. About mid-March in Pullman the cells begin to increase in size in the plane of their short axis (e.g., perpendicular to the surface). As this increase in size continues strands appear across the short axis of some cells. These strands (presumably trabeculae) have a typical cellulose stain reaction (Mullen, 1928). By early April the cells have almost reached their mature size and each cell has cellulose thickenings, deposited in layers along the inside and lateral walls. In general the outer cell walls show no thickenings, though frequently a tuft-like mass of cellulose strands may appear on the inner surface (Mullen, 1928).

The mature condition, observed in late April or early May, is essentially that just described. There is only a slight increase in cell size. However, there is a distinctly different staining reaction. During April the thickened walls are impregnated with lignin; until this is complete the staining reaction is not uniform, varying with the amount of lignin present. When the impregnation is complete a deep red color results from staining with safranin or treatment with concentrated HCl and phloroglucin.

Members of the *Allium acuminatum* alliance are dormant during the hot dry months of summer and early fall. It has been demonstrated repeatedly, with pressed specimens, that the resistant layer is responsible for conserving moisture in the fleshy cataphyll during this period. Flowering plants collected and pressed during the spring have bulbs that will sprout the following year provided the resistant layer is not disrupted by the pressing. This is true even when the specimens are dried in a drying cabinet for up to three weeks. Numerous herbarium specimens of all species in the alliance show sprouts that were formed a year after the plants were pressed. In bulbs where the resistant layer is disrupted, the fleshy cataphyll dries out and no sprouting occurs the following year.

The resistant layer, while very conspicuous and highly developed, is not unique to the *Allium acuminatum* alliance. Treatment with concentrated HCl and phloroglucin indicates that the inner epidermis of the inner leaf base forms a sclerified resistant layer in *A. crenulatum*, *A. glandulosum*, and *A. tribracteatum* Torr., a non-rhizomatous member of the *A. falcifolium* alliance. The resistant layer in these species, however, is thin and does not show the prominent cellular reticulation found in the *A. acuminatum* alliance, but it serves the same protective function. This is easily observed in herbarium specimens, as these species also show the ability to sprout a year or more after being pressed and dried, provided they are not crushed in the process.

Bulbs, in the garden, root and sprout after the fall rains begin in early to mid-November. Bulbs of all species maintain their dormancy even when watered during the summer, though such plants may sprout two to three weeks ahead of those receiving no summer water. In an attempt to break the dormancy, dry, mature bulbs of several species were planted in sand and subjected to 4°C with once-a-week watering. This treatment was begun in late July, 1968 and continued for eight weeks, after which the bulbs were moved to the greenhouse and watered as needed. When these bulbs were compared with those grown continuously in the greenhouse where watering began in late November, the sprouts of the experimental group appeared above ground less than two weeks before those of the greenhouse specimens. The fact that bulbs receiving adequate summer moisture do not sprout earlier indicates that a very strong dormancy, which can be broken only after a fairly long rest period, prevails in these species.

Non-rhizomatous members of the *Allium acuminatum* alliance, as is common in bulbous monocotyledons, produce two types of bulbs each year. The first is the single bulb arising as an axillary bud from the inner leaf base; since this bulb serves to continue the plant that produced it, it is termed a renewal bulb (Mann, 1960). As the axis of the renewal bulb develops during the first spring, forming a sheath, fleshy cataphyll, and two non-fleshy cataphylls, one or more buds may appear

in the axils of each of the newly formed cataphylls. These buds will also develop into bulbs, and, as they serve for vegetative multiplication, they are termed increase bulbs (Mann, 1960).

If a small number (two to four) of increase bulbs are formed, they develop only in the axil of the inner cataphyll, but if a larger number are formed both cataphylls are usually involved. Development of the increase bulbs occurs simultaneously with the further development of the renewal bulb. If an increase bulb bud forms in the axil of the inner cataphyll, it will develop two foliage leaves, as does the renewal bulb. A bud developing in the axil of the outer cataphyll, however, would first produce a non-fleshy cataphyll, corresponding to the inner cataphyll of the renewal bulb, in addition to the two foliage leaves. In both cases the leaves of the increase bulbs are included within the sheath, fleshy cataphyll and one or both non-fleshy cataphylls of the renewal bulb. Subsequently, in the second spring, the inner leaf base of the renewal bulb and each increase bulb forms a resistant layer, inside of which a new sheath and fleshy cataphyll develop. In this manner both types of bulbs produce their own renewal bulbs for the following year. The actual positions of the renewal bulbs depend on whether or not the shoot axis involved produces an inflorescence. The original renewal bulb and, commonly, one or more of the increase bulbs will flower. Those bulbs producing an inflorescence form a renewal bulb in the axil of the inner leaf base, while those not flowering apparently produce the renewal bulb terminally on the shoot axis. Separation of the renewal bulbs occurs when the surrounding leaf tissues disintegrate, leaving each bulb invested by its own resistant layer. By this stage it is usually impossible to distinguish between the original renewal and increase bulbs as they are all approximately the same size.

Considerable difference exists in the *Allium acuminatum* alliance as to the number of increase bulbs formed in any one year. Under field conditions it was observed that vegetative multiplication may occur infrequently, with one or more years between the production of successive increase bulbs. For example, *A. davisiae* from the Mojave desert may have a single bulb invested by the resistant layers of ten or more growing seasons, indicating that no increase bulbs were formed during this period. At the other extreme, *A. hyalinum*, growing under moist soil conditions on the border of the San Joaquin Valley, may have as many as six increase bulbs produced in a single season. Generally, plants collected in the field tend to have one or two increase bulbs formed each year. Plants from the same populations, grown under more favorable soil and water conditions in the garden, have larger bulbs, increase annually, and, in *A. hyalinum* and *A. amplexans*, at least, may produce as many as eight to twelve increase bulbs per year.

In addition to differences in the rate of vegetative multiplication, the morphology of the non-rhizomatous species, or individuals within species,

may differ in detail from the general type described. Some individuals of *Allium acuminatum*, for example, have three cataphylls and three foliage leaves. This would add a C3 and L3 to Figure 1, but otherwise no difference is observed from the previous description; likewise *A. dichlamydeum* has two or three cataphylls and three to six leaves. Considerable variation is also observed in the size of mature bulbs; flowering size bulbs of *A. crispum*, *A. dichlamydeum*, and *A. praecox* are commonly 1–2 cm in diameter, while those of *A. hyalinum* and *A. hickmanii* seldom exceed 6 mm. The other species of the alliance fall between these extremes. Again, while these differences in detail exist, the general morphology is the same in all of the non-rhizomatous species.

The rhizomatous species, as represented by *Allium unifolium* (fig. 2), do not differ significantly from each other, regardless of the length of the rhizome, and, except for the rhizome (Rz) have the same general morphology as the non-rhizomatous species. The bulb at the end of the rhizome (Rz) in Figure 2 represents the stage observed in late spring prior to anthesis. This is a renewal bulb developing in the axil of the inner leaf base (L2). Here, as in the non-rhizomatous species, the in-

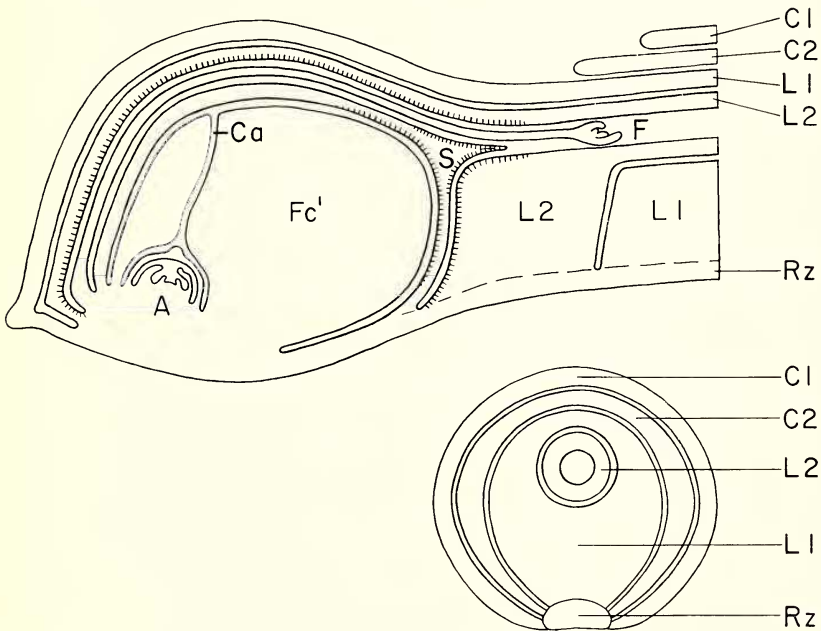


FIG. 2. Median-longitudinal section through a rhizome and new bulb and cross section of a rhizome of *Allium unifolium*: A, apical meristem; Ca, canal; S, sheath; F, scape (current year); Fc', new fleshy cataphyll; L1, L2, leaf bases; C1, C2, cataphyll bases; Rz, rhizome.

florescence (F) terminates the shoot axis and the sheath (S) and fleshy cataphyll (Fc') are the first leaves of the secondary axis. The fleshy cataphyll and resistant layer of the preceding year, corresponding to Fc and R in Figure 1, are not shown because the elongating rhizome leaves them behind. As the bulb continues to develop, two cataphylls are produced by the apical meristem (A) and grow into the tubular canal (Ca) formed by the open end of the fleshy cataphyll. Subsequently, the buds of one or two increase bulbs may develop in the axil of the inner cataphyll. During this period the plant flowers and the leaf and rhizome tissues outside the new resistant layer (indicated by shading) disintegrate. Like the non-rhizomatous species, the rhizomatous ones become dormant after flowering and maintain their dormancy during the warm, dry summer months.

In early spring of the following year roots develop below A (fig. 2) and shortly thereafter the cataphylls and leaves resume growth, breaking through the resistant layer above the canal. With the resumption of growth, one, two, or three rhizomes develop from near the shoot apex (one rhizome developing for the renewal bulb and each increase bulb formed the preceding year). These break through the resistant layer adjacent to the rootpad carrying with them the apical meristem and leaf and cataphyll bases, which form tubular extensions as they grow. Growth of the rhizome and the tubular extensions is presumed to be due to intercalary meristems. Cell division has not been observed and, because of the highly condensed nature of the shoot, the exact relationship between the apical meristem and the rhizome is unclear. However, the shoot apex is certainly carried along by the elongation, if not the division of cells below those that can properly be considered to be included in the apical meristem.

The old fleshy cataphyll and resistant layer are again left behind by the elongating rhizomes. As in the non-rhizomatous species the fleshy cataphyll disintegrates with its stored nutrients being, presumably, translocated to the new growth.

Shortly after the rhizome begins to grow the growth potential of the cataphylls is exhausted and, as they cease to elongate, the rhizome and leaf bases break through them. Thus, when the rhizome stops growing its tip is surrounded by the outer leaf base as all tissues outside it have been left behind.

Few roots develop along the rhizome, and the rootpad formed by the old bulb remains functional throughout the growing season. It is connected to the rhizome by vascular bundles.

The leaf and cataphyll bases differ from those of the non-rhizomatous species in being asymmetrical. The connection of the leaf base to the rhizome is elongate on the upper side of the rhizome (fig. 2). In addition to the asymmetrical connection, the leaf base, in this area, is thickened by the presence of substantial amounts of parenchyma, which is absent

in the rest of the leaf base. As with the fleshy cataphylls, this parenchyma tissue apparently acts in a storage capacity. Development of the renewal bulb of the following year's plant occurs during and immediately after the growth of the rhizome. Disintegration of the leaf tissues follows as the new fleshy cataphyll matures and this disintegration, presumably, contributes nutrients and/or water to the development. In the species with short rhizomes the elongate, fleshy portion of the leaf base is considerably reduced, reflecting the reduced length of the rhizome.

The scape (F) originates at a point along the union between the sheath and the inner leaf base, just as it did in the non-rhizomatous species. Generally the scape grows up the cylindrical passageway formed by the inner leaf base and through the canal in the preceding year's fleshy cataphyll, before it appears above ground. In *Allium unifolium*, however, due to the length of the rhizome, the scape frequently breaks out of the leaf bases below the old fleshy cataphyll, appearing above ground at some distance from the leaves. In field collections of this species only one scape is produced, regardless of the number of rhizomes formed by a single bulb. Further it was determined that the original renewal bulb produces the scape while the increase bulbs, carried on separate rhizomes, produce only somewhat depauperate leaves. Populations grown in the garden at Stockton often develop two or three scapes, but even here the scape associated with the renewal bulb predominates in size and the others are significantly smaller.

The length of the rhizome is one of the most distinctive features separating rhizomatous species of the *Allium acuminatum* alliance. In addition, the species with short rhizomes, including *A. crenulatum* of the *A. falcifolium* alliance, tend to have only two or very rarely three leaves; *A. unifolium*, on the other hand, may have up to six. The bulbs of all species except *A. mirabile* are ovate, but there is considerable variation in size. In *A. unifolium* the bulbs are 1.0–1.5 cm in diameter, while in *A. bolanderi* and *A. dictuon* they are less than 1 cm in diameter. In *A. crenulatum* the bulbs are larger, 1–2 cm in diameter, but it should be noted that several of the species in the *A. falcifolium* alliance have bulbs that are larger than those of any of the species in the *A. acuminatum* alliance. In *A. mirabile* the bulbs are elongate-ovate and very irregular in shape, superficially resembling small tubers. The long axis of these bulbs rarely exceeds 1 cm. In spite of these differences in detail the rhizomatous species, like the non-rhizomatous ones, have a remarkable similarity in their bulb morphology.

The bulbs of *Allium glandulosum*, the second species with long rhizomes, superficially resemble those of *A. unifolium*, but considerable divergence in morphology between the two species is observed. *Allium glandulosum* flowers from mid-summer to fall rather than in the spring and, as a result its seasonal development is at least three months later than any of the other species investigated. The developmental sequence,

except for the time lag, is similar to *A. unifolium*; there are, however, some rather important differences in the rhizome. The meristem of the renewal bulb is not passed to a rhizome, but rather it develops within the confines of the current year's leaf bases in the manner of the non-rhizomatous species investigated. Thus the continuity of the main bulb is maintained. The rhizomes carry the apical meristems of the increase bulbs. Furthermore, the apical meristem of the increase bulb produces a succession of asymmetrical fleshy cataphylls beyond the attachment of the leaf bases, each succeeding cataphyll breaking through the base of the previous one as the rhizome elongates. The rhizome in *A. glandulosum* is 8–12 cm long and may branch as secondary increase bulbs form from buds in the axils of one or more of the succession of fleshy cataphylls. As with *A. unifolium*, new increase bulbs are borne terminally on the rhizome, or its branches, but in their development they have left behind any direct association with the bases of foliage leaves or the passageway through which the leaves and scape emerge. It is as if the apical meristem (A in fig. 2) continues to produce successive fleshy cataphylls, only the final one or ones of which enter into the formation of the mature increase bulb.

Normally a single scape is formed by *Allium glandulosum* and it is associated with the main bulb. Just as in the other species, the scape is terminal on the shoot axis and is located along the union between the inner leaf base of the current bulb and the sheath, which represents the first leaf of the axillary renewal bulb. Additional scapes associated with increase bulbs are rarely produced. They arise terminally on the axis of the increase bulb in a position corresponding to the scapes in *A. unifolium* (fig. 2). The additional fleshy cataphylls in *A. glandulosum* mean that the scape is more remote from the bulb formed at the tip of the rhizome, but otherwise no difference is observed from the position of the scape in *A. unifolium*.

DISCUSSION AND CONCLUSIONS

Judged by the organization of their bulbs, the non-rhizomatous species of the *Allium acuminatum* alliance form a closely related and natural group. As noted earlier, all of the plant organs in the non-rhizomatous species are found in the same sequence in the rhizomatous ones. Furthermore, these structures are in the same relative positions, except that the rhizome carries the leaf and cataphyll bases, and all of the parts inside these organs, outside the confines of the preceding year's fleshy cataphyll and resistant layer. In the non-rhizomatous species, on the other hand, all growth occurs within the confines of the old fleshy cataphyll and resistant layer. Except for the rhizome, the general development and morphology of the bulb are identical in both groups.

In comparing the morphology of members of the *Allium acuminatum* alliance with that reported by Mann (1960) for the European section

Molium, a number of similarities as well as striking differences are noted. The first leaves of a main or renewal bulb in sect. *Molium*, corresponding in position to the sheath in *A. acuminatum*, are a pair of bladeless leaf bases that become fused along their adjacent epidermal layers. Because the inner epidermis of the outer of these two leaves becomes sclerified, Mann termed them protective leaves. Functionally the protective leaves correspond to the resistant layer in the *A. acuminatum* alliance, but the derivation of the two structures is dissimilar. The resistant layer of the *A. acuminatum* alliance develops from the inner leaf base of the mother bulb, or primary axis, while the protective leaves of sect. *Molium* develop as the first leaves of the renewal bulb, or secondary axis. As a result, the remains of the scape are included within the resistant layer in the former and outside the protective leaves in the latter.

The protective leaves of the increase bulbs in sect. *Molium* are surrounded by a second type of bladeless leaf, absent in the renewal bulb, which Mann called a prophyll. If, in fact, the protective leaves correspond to the sheath in the *Allium acuminatum* alliance, then there is no organ corresponding to the prophyll. This interpretation is supported by the presence of a sheath in both the renewal and increase bulbs of the *A. acuminatum* alliance and the presence of protective leaves around both types of bulbs in sect. *Molium*. The *A. acuminatum* alliance has no type of leaf that is present in the increase bulbs, but lacking in the renewal bulb, thus corresponding to the prophyll in sect. *Molium*.

The protective leaves in sect. *Molium* surround a food storage leaf that corresponds in structure and function to the fleshy cataphyll of the *Allium acuminatum* alliance. Inside the food storage leaf is a single bladeless sprout leaf that corresponds to the cataphylls in Figure 1. Mann reported only a single sprout leaf in each bulb of sect. *Molium* while, as pointed out earlier, two or three cataphylls occur in each bulb of the *A. acuminatum* alliance.

The bases of the foliage leaves are similar in both groups, though the bulbs of sect. *Molium* tend to have a larger number of leaves per bulb. Above ground, the leaf blades of sect. *Molium* are larger and more prominent.

Branching of the shoot axis is more prolific in sect. *Molium*. In addition to the branches terminated by increase bulbs, there are from one to five branches terminated by inflorescences and one terminated by a renewal bulb. In the *Allium acuminatum* alliance, on the other hand, only two branches are found in addition to those bearing increase bulbs, one terminated by an inflorescence and the other by a renewal bulb.

The development of increase bulbs is similar in both groups, but the position and developmental sequence are different. In sect. *Molium* the new renewal bulb is differentiated in the axil of the upper foliage leaf in early autumn. Following the formation of this renewal bulb, the increase

bulbs develop in the axils of the foliage leaves immediately below it. Generally these increase bulbs do not develop leaves in the spring after they are differentiated, but rather develop their first foliage leaves in the following spring, some eighteen months later. Only under the most favorable garden conditions were leaves and inflorescences formed in the first year. The increase bulbs varied greatly in size, but were usually very much smaller than the renewal bulbs.

In the *Allium acuminatum* alliance the increase bulbs develop concurrently with the main bulb axis and prior to the differentiation of a new renewal bulb. The increase bulbs develop in the axils of the cataphylls and invariably produce green foliage leaves and, commonly, inflorescences in the spring following their initiation. Because of the simultaneous development of the increase bulbs and the main bulb, and the early development of foliage leaves, the increase bulbs are approximately the same size as the renewal bulb at the end of their first growing season. In both groups the separation of the renewal and increase bulbs occurs when the surrounding leaf tissues disintegrate.

Mann concluded from his investigation that the species in sect. *Molium* form a closely related natural group. Members of the *Allium acuminatum* alliance also are closely related. The general bulb morphology of these two groups, as would be expected, is similar. Bulbs of both groups are composed of several distinct types of leaves without intergrading forms. They are ecologically specialized for maturation in the spring and long periods of summer dormancy. Along the same line, the enclosure of each bulb by a firm sclerotic layer has been demonstrated to be of ecological significance in enabling the bulbs to resist desiccation during dormancy.

The differences in these two groups, however, particularly in the origin of the resistant layer, the order of development of the increase and renewal bulbs and the lack of a prophyll, indicate that members of the *Allium acuminatum* alliance have in common a number of important characters that separate them from sect. *Molium*. The fact that *A. crenulatum* and *A. glandulosum* have an organization and developmental sequence similar to the rhizomatous species of the *A. acuminatum* alliance indicates further that the three alliances involved are also closely related. If, as seems probable, the non-rhizomatous species of the *A. falcifolium* and *A. kunthii* alliances have an organization similar to the non-rhizomatous members of the *A. acuminatum* alliance, this will be further evidence of a close relationship among the New World species of *Allium*.

SUMMARY

Bulb organization and seasonal development are described for the rhizomatous and non-rhizomatous species of the *Allium acuminatum* alliance and for the rhizomatous species *A. crenulatum* of the *A. falcifolium*

folium alliance and *A. glandulosum* of the *A. kunthii* alliance. The two types have a highly similar morphology except for the rhizome. Except for *A. glandulosum*, the species begin growth in the late fall or winter, flower from February to June and are dormant throughout the summer. *Allium glandulosum* blooms in the summer and fall and there is a corresponding time lag in its development. Four distinct types of leaves make up the bulb including: a sheath, a fleshy storage cataphyll, bladeless leaf sheaths or cataphylls, and foliage leaves. Sclerification of the inner epidermis of the inner leaf base forms a heavy, cellular-reticulate, resistant layer in the *A. acuminatum* alliance. The resistant layer effectively prevents desiccation of the bulb. The shoot axis annually produces two kinds of bulbs: a renewal bulb differentiates in the the axis of the upper foliage leaf, serving to continue the plant, and one or more increase bulbs may differentiate in the axils of the cataphylls, serving for vegetative multiplication. Bulb size appears to be one factor that triggers the differentiation of increase bulbs and determines how many will develop. In comparing bulb morphology of the species investigated with the bulbs of the European sect. *Molium*, it was found that they differed in the origin of the resistant layer, the development of increase bulbs, and the absence of a fifth type of leaf, the prophyll, present in sect. *Molium*.

TABLE 1. SOURCES OF MATERIALS USED IN THE INVESTIGATION OF BULB MORPHOLOGY IN WESTERN AMERICAN ALLIUMS. (Vouchers have been deposited at CPH and WS.)

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- A. acuminatum*. Wash., Whitman Co., 2 mi. N of Almota, *McNeal* 377. Calif., Trinity Co., 2.8 mi. E of Forest Glen, Rattlesnake Creek, *McNeal* 504.
- A. amplexens*. Calif., Del Norte Co., 9.4 mi. N of Gasquet, *McNeal* 412; Mariniposa Co., 2.1 mi. N of Merced River on Rte 49, *McNeal* 490.
- A. bolanderi*. Calif., Shasta Co., 1.1 mi. S of Round Mt., *McNeal* 399.
- A. crispum*. Calif., San Benito Co., Rte. 25, 4.1 mi. S of Tres Pinos, *McNeal* 495.
- A. davisiae*. Calif., Kern Co., Rte. 14, 3 mi. S of Mojave, *Ownbey* 3502.
- A. dichlamydeum*. Calif., Sonoma Co., Rte. 1, 3 mi. N. of Bodega Bay, *McNeal* 411.
- A. dictyon*. Wash., Columbia Co., Blue Mts., 0.5 mi. N of Weller Butte, *McNeal et al.* 415.
- A. hickmanii*. Calif., Monterey Co., Monterey, Veterans Memorial Park, *McNeal* 484.
- A. hyalinum*. Calif., Stanislaus Co., Rte 132, 1.5 mi. W of La Grange, *McNeal* 393.
- A. lacunosum* var. *lacunosum*. Calif., Marin Co., Tiburon Peninsula, *McNeal* 500.
- A. lacunosum* var. *micranthum*. Calif., San Benito Co., above entrance station, E side Pinnacles National Monument, *McNeal* 496.
- A. mirabile*. Calif., Siskiyou Co., 2.6 mi. W of Hilt, *Ownbey and Mingrone* 3490.
- A. peninsulare*. Calif., Kern Co., Rte. 178, 1.5 mi. E of Onyx, *McNeal* 389; San Mateo Co., Jasper Ridge, Stanford University, *Raven s.n.* in 1968.
- A. praecox*. Calif., San Diego Co., 3.5 mi. E of Chula Vista, *McNeal* 390.
- A. serratum*. Calif., Stanislaus Co., Del Puerto Canyon, *McNeal* 395.
- A. unifolium*. Calif., San Luis Obispo Co., Santa Barbara Rd., Atascadero, *Hardham* 5502.
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NOTES AND NEWS

IMPATIENS PARVIFLORA IN BRITISH COLUMBIA.—*Impatiens parviflora* DC., a native plant of Central Asia, has become established in Europe and eastern Canada. It has not, however, been reported from western North America, although it has now been collected from two places in southwestern British Columbia. Moreover, the population at one of these locations has maintained itself for at least twenty years. The first collection was made in 1949 (*J. W. Eastham 16,477*, UBC). Eastham found a small plant growing in sandy soil between the beach and the road at Spanish Banks, a popular beach on the north side of Point Grey peninsula, Vancouver, B.C. He noted on the herbarium sheet that there were several, more robust, plants growing in the wooded area on the opposite side of the road. When this area was revisited in 1972, the species was well established in the woods, but no plants were found on the beach side of the road (*Barkworth 527*, WS).

In 1972, I found this species at Lions' Bay, 8 miles north of Horseshoe Bay, West Vancouver, approximately 15 miles due north of Spanish Banks (*Barkworth 513*, 523, WS). Here, too, the plants were growing beside a road, highway 99, and near a developed area, Lions' Bay community. The road has been cut into the hillside, creating a steep gravel bank on the east side. Several plants of *Impatiens parviflora* were growing on a small gravel pile located at the foot of this bank. They were more abundant on the east side of the gravel pile where they received some degree of protection. Apart from this topographic protection the area is very open. In addition the road bank is not very stable. Fifty feet from the *I. parviflora* population there were frequent small falls of gravel, even on a dry summer day. The highway department presents yet another hazard. Several sections of the road are being improved at the present time, so the site may be destroyed by highway work crews. It appears, therefore, that the success of the species in this area will depend, in large part, on its becoming established in a 'safer' location before the present site is destroyed.—MARY E. BARKWORTH, Department of Botany, Washington State University, Pullman 99163.